



Assisted colonization in a changing climate: a test-study using two U.K. butterflies

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Abstract

Recent climatic change in temperate regions has been rapid and there is mounting speculation that species are failing to keep track of suitable climate, perhaps necessitating assisted colonization for some species. An inability to spread into new areas may result in large reductions in species' ranges in the future, and threaten the survival of some species. Here we use "species-climate" models to predict suitable sites for introductions beyond current range margins, using two U.K. butterfly species. We introduced *Melanargia galathea* (marbled white) and *Thymelicus sylvestris* (small skipper) into two sites in northern England, ~65 and ~35 km beyond their then-range margins, respectively, to sites that were predicted to be climatically suitable and that appeared to contain suitable habitat for the species. Both introduced populations grew and expanded their range over 6 years (2001–2006; still thriving in 2008), suggesting the existence of a colonization lag and providing evidence that well-planned assisted colonization can be successful. We suggest that assisted colonization may be a feasible and cost-effective means of enabling certain species to track climatic change.

Introduction

There is widespread evidence that species' distributions have recently shifted toward higher latitudes and elevations as the climate has warmed (Parmesan *et al.* 1999; Crozier 2003; Konvicka *et al.* 2003; Parmesan & Yohe 2003; Root *et al.* 2003; Wilson *et al.* 2005; Franco *et al.* 2006; Hickling *et al.* 2006; Thomas *et al.* 2006; Merrill *et al.* 2008). Population changes have also occurred, in line with projections based on recent climatic change (Roy *et al.* 2001; Green *et al.* 2008; Gregory *in press*). However, it has been suggested that many species are not shifting their distributions as fast as the rate at which the climate itself is changing (Warren *et al.* 2001; Hill *et al.* 2001; Midgley *et al.* 2006; Menéndez *et al.* 2006). This is particularly the case for habitat specialists and species with poor

dispersal ability, for which human-dominated landscapes may present serious barriers to colonization (Warren *et al.* 2001); the extent to which habitat generalists might also be lagging behind climatic change is less clear (Hill *et al.* 2001).

The negative impact of climatic change on biodiversity, time lags in response and the (in)ability of species to move through the landscape are important policy issues (Sutherland *et al.* 2006). Adaptation of land use, improved habitat management and restoration of semi-natural habitats are the current focus of efforts to improve landscape quality, connectivity, and permeability for species dispersal (e.g., Boitani *et al.* 2007). Assisted colonization has also been proposed as a pragmatic and cost-effective conservation tool to facilitate the movement of certain species across landscapes, if they are

themselves unable to keep track of a rapidly changing climate, and providing that there would be little risk arising from such translocations (Hulme 2005; Hunter 2007; McLachlan *et al.* 2007; Hoegh-Guldberg *et al.* 2008).

Most of the existing “evidence” for colonization lags is largely based on conjecture, and direct evidence that populations could survive beyond their currently expanding range boundaries is rare (Menéndez *et al.* 2006). To this end, we introduced populations of two grass-feeding British butterfly species, *M. galathea*, Linnaeus, 1758, (marbled white) and *Thymelicus sylvestris*, Poda, 1761, (small skipper), beyond their currently expanding northern range margins, in northern England.

Specifically, our objectives were (1) to establish, using climate-envelope models, whether there were potential areas of suitable climate for the two species beyond their current range margins, (2) to determine, by means of artificial introductions (assisted colonizations), whether such areas could support viable populations, and (3) for *M. galathea*, to examine the performance of the introduced population relative to that in areas of recent natural range expansion. The introductions would therefore provide a first assessment of the potential role of such an approach to establish self-sustaining populations of species currently experiencing (or projected to experience) colonization lags resulting from rapid climatic change. The study species are used to test the principle of the approach, rather than being important conservation targets in their own right. Thus, we address the issue of whether the “translocation and establishment of species

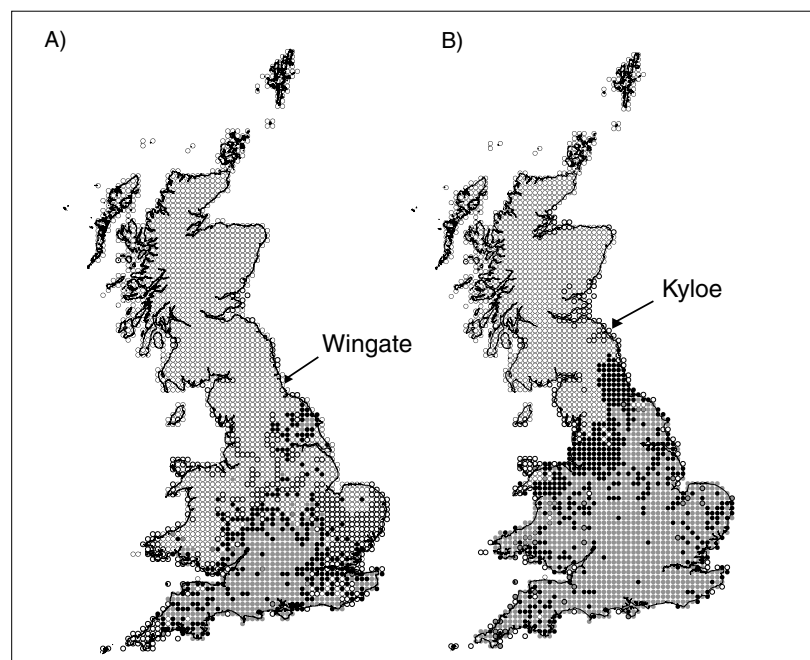
[is] technically feasible” (Hoegh-Guldberg *et al.* 2008) for these two species.

Materials and methods

Study species

Both study species are relatively good dispersers, and are currently expanding their ranges northwards in Britain (Figure 1). *Melanargia galathea* was recorded in 66% more 10 km squares during a census in 1995–1999 compared with an earlier census in 1970–1982 (Asher *et al.* 2001), and the number of recorded grid squares increased by 37% in *T. sylvestris* over the same time period (Asher *et al.* 2001). The caterpillars of both species feed on grasses. In northern England, *M. galathea* is mainly restricted to unimproved chalk and limestone grasslands; both the geology and remaining semi-natural vegetation are discontinuous, so we might therefore expect that barriers to dispersal could interrupt the northwards expansion of this species. *Thymelicus sylvestris* is less restricted to a particular habitat type, and its main larval host plant is *Holcus lanatus*, a grass species that is common and widespread, including on road verges and other marginal habitats. Therefore, the issue for this species is whether dispersal has been sufficiently rapid for it to keep up with climatic change. Among a number of possible candidate species, the two study species were chosen mainly because they both feed on widespread host plants (grasses) and occur in habitats that also occur to the north of the species’

Figure 1 Recent range expansion for (A) *M. galathea* and (B) *T. sylvestris* in the United Kingdom at a 10 km grid resolution. Recorded distributions of species are from Asher *et al.* (2001). Hollow circles represent unoccupied grid squares, black circles represent grid squares newly occupied in 1995–1999 and gray circles indicate grid squares occupied between 1970 and 1982. Sites of introduction at Wingate Quarry Co., Durham for *M. galathea* and Kyloe Quarry, Northumbria for *T. sylvestris* are marked.



current distributions, so it is reasonable to suppose that climate could be a factor limiting their distributions.

Areas of climate suitability beyond the range margins

We used climate response surface models to fit species' distributions across Europe to three bioclimate variables (mean temperature of the coldest month, annual temperature sum in day-degrees $> 5^{\circ}\text{C}$, moisture availability) using methods described in detail in the supporting information and elsewhere (Hill *et al.* 1999; Huntley *et al.* 2008). We then applied the models to Great Britain to predict 10-km grid cells beyond the species' range margins that appeared climatically suitable (simulated probability of occurrence is greater than a threshold value, following Hill *et al.* 1999), yet remained unoccupied. Model output indicated that climatically suitable but unoccupied areas occur in limited areas of northern England, coastal Scotland and north-west Wales for *T. sylvestris*, and in east and south-west England and coastal regions of Wales and northern England for *M. galathea* (Figure S1).

Introduction of *M. galathea* and *T. sylvestris* beyond their current range limit

To test whether areas of apparently suitable climate beyond the current species' ranges can support populations of the two species, separate introductions were made of each species beyond their respective northern range limit. For both species, adults (1:1 sex ratio) were collected from sites in North Yorkshire and translocated either to Wingate Quarry Local Nature Reserve, Co. Durham (*M. galathea*; OS grid reference NZ3737; Figure 1A), or to Kyloe Quarry, Northumberland (*T. sylvestris*; OS grid reference NU0440; Figure 1B). Both release sites were disused quarries, containing plenty of breeding habitat, and were chosen after discussion with local experts. According to the response surface models, both sites were in areas of apparently suitable climate (probability of occurrence exceeded the threshold value in both cases). Approximately 500 individuals of *M. galathea* were translocated in early July 2000. Approximately 400 individuals of *T. sylvestris* were translocated in late July or early August in 1999 and a further 200 individuals were released in late July 2000. Free-flying individuals were netted at the donor populations, caged, transported to the release sites, and released at a single point the following day.

Monitoring the introduced populations

During the two species' flight periods we monitored the persistence of each species by searching for adults. We

recorded occurrences of individuals within and beyond the release sites every year from 2001 to 2006, undertaking extensive searches of the entire release area and all of the suitable habitat within 3- to 4-km radius of the release, recording the location of individuals using handheld GPS recorders. Within the immediate area of the release sites, we undertook searches in different areas concurrently to minimize multiple recording of individuals. This provided us with a "total" population count on each survey day in the release areas. From these data, we also calculated dispersal functions for the two species at their climatic range margins and compared these with similar functions estimated from recent natural range expansions. We also used these data to calculate population range polygons and population kernels to examine changes in range size and structure over 6 years. Population extent was estimated for each year using HRE: the home range extension for ArcView (Rodgers & Carr 1998). We calculated kernel polygons for population density using the default parameters (a volume contour with a smoothing factor of 1 and fixed smoothing) in Rodgers & Carr (1998). Limited census data were collected for 2007 and 2008.

We monitored the population of *M. galathea* every few days during the main flight period each year. For *T. sylvestris*, we did not collect data as often but still surveyed the population several times during the main flight period for each year (except 2005, when only one visit was made).

For *M. galathea*, we also undertook regular transects every 3–4 days during the flight period using standardized Butterfly Monitoring Scheme methods (Pollard & Yates 1993). We set up a 1,550-m transect divided into 11 sections to calculate changes in density within and between years. We compared population growth at the introduced site with seven newly colonized UKBMS (U.K. Butterfly Monitoring Scheme; www.ukbms.org) sites. We also included an additional UKBMS site (Waterperry, U.K. grid reference SP0069) into this analysis that had a population of *M. galathea* that had declined to near-extinction in 1982 (peak count of two individuals) before recovering. Of these eight sites, four showed population growth (from linear regressions of annual $[\log_e\text{-transformed}]$ population density against time) in high-quality habitats; with the remainder either showing no evidence for growth or variable numbers in suboptimal habitat. We introduced *M. galathea* into apparently highly suitable habitat and so we compared population growth with that of colonized sites in high-quality habitats farther south (see Figure 3 for locations of these colonized sites). We estimated the geometric growth rate of each population from the slope of the relationship of $(\log_e\text{-transformed})$ UKBMS population

index (www.ukbms.org) versus years since colonization/introduction. We compared differences in the growth of colonized and introduced populations from the “site \times year” interaction term of a generalized linear model, incorporating year and population index as variables and site as a factor.

Results

Site assessment and introduction

Although both species have expanded northwards in recent decades (Figure 1), unpopulated locations were found that were predicted to be climatically suitable (Figure S1). For both species, apparently suitable habitats could be found relatively easily within these areas: a disused limestone quarry with established grassland vegetation was selected for release in the case of *M. galathea*, and another disused quarry and adjacent grassland supporting *H. lanatus* for *T. sylvestris*. Therefore, the first part of the feasibility study suggested that potential suitable conditions for the two species existed outside their then-current distributions.

Both introductions were successful. Following introduction of *T. sylvestris* in 1999 and 2000, and of *M. galathea* in 2000, populations of both species were still present at sites to 2008, 8 years (= eight generations) after being translocated.

Dispersal and population expansion

Following the experimental introductions, the distribution extent of both study species increased over time, indicating population spread. We assessed changes in distribution extent from polygons encompassing 95% of recorded occurrences over the season (to exclude the few long-distance dispersing individuals) for the period 2001–2006. The distribution extent of *M. galathea* increased from 7.2 to 17.8 ha, and that of *T. sylvestris* from 0.17 to 3.64 ha over the 6 years following the initial introductions.

Dispersal data for the year of the initial releases of the population of the two species adequately fitted a negative power function in both cases (*M. galathea*: $I = 4.85 \times 10^{-3} D^{-1.499}$, $R^2 = 0.84$, $F_{1,15} = 83.81$; *T. sylvestris*: $I = 7.13 \times 10^{-3} D^{-1.260}$, $R^2 = 0.61$, $F_{1,14} = 21.81$, where I is the probability of an individual moving a distance D [km]). Power functions have relatively long tails of a small number of individuals moving long distances (compared, for example, to a negative exponential), and these individuals could be essential to the expansion rates of geographic ranges (Lensink 1999). However, the longest-distance dispersal events we recorded did not result in population

establishment; all long-distance dispersers were males. Seven *M. galathea* individuals (1.7% of records) dispersed > 1 km from the release site in the year of release, and the maximum dispersal distance we recorded was 3.0 km (we were informed of an individual 12.7 km from the release site that probably originated from the translocation). In subsequent years, only 2% of records were of individuals > 1 km from the release site, and 95% of individuals recorded in 2006 were within 500 m of where the release had taken place 5 years earlier.

For *T. sylvestris*, 95% of all individuals sighted in 2001 were within 200 m of the release site. While the mean distance of individuals from the release site increased over time, only four individuals were recorded > 1 km from the release site, all in 2006. No longer-distance population establishments were recorded by us or others, for either species.

To summarize, both introduced populations did spread consistently, and at a similar rate to other expanding butterfly species in the United Kingdom (Hill *et al.* 1996) but the < 1 km/year rate of expansion was much lower than the ~ 4.5 km annual northwards shift of isotherms in northern Britain (Franco *et al.* 2006), suggesting that a lag between climate and distribution change is developing in our two study species.

Population growth

The peak population count of *M. galathea* at the introduction site (Figure 2) and the density of *M. galathea* along the fixed transect (Figure 3) both increased steadily. These provided geometric growth rates estimates of 0.37 (peak count) and 0.18 (transect). There was no difference between the population growth rate of the introduced site and any of the naturally colonized sites (site \times year interaction of the GLM with site as a factor, $df = 1$, 14, $F < 1.92$, $P > 0.05$ in all four cases), suggesting that the introduced population grew at a similar rate to other newly colonized sites (Figure 3). The intercept of the introduced population (Wingate) is higher than naturally colonized sites because natural colonizations are initiated by much smaller numbers than the numbers of individuals we released.

Discussion

The successful establishment and spread of the populations of *M. galathea* in Durham and of *T. sylvestris* in Northumberland suggest that the climate in the two places has been suitable in the period since introduction, and that the distributions of these species were lagging behind current climate warming. The more detailed

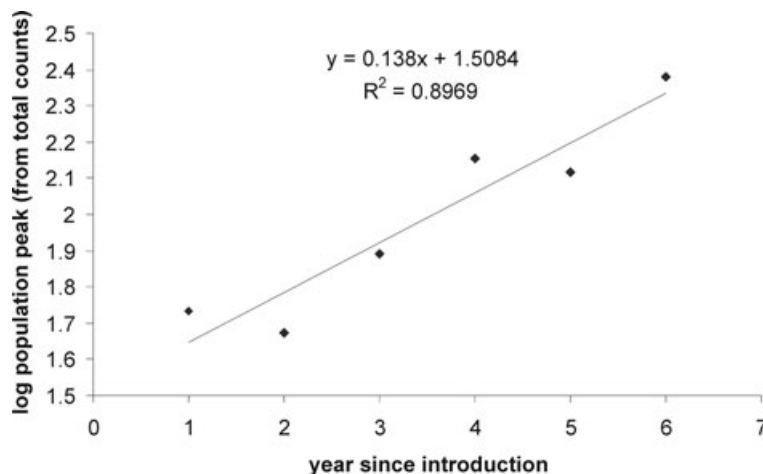


Figure 2 Changing peak population count of *M. galathea* following their introduction in 2000 to Wingate.

monitoring of the *M. galathea* population showed a steady increase in population size over time, which was not different from the rate of population growth further south, where the species was expanding naturally. Similarly, the introduced *T. sylvestris* population established and spread from the release point. Conditions were suitable for establishment ~ 65 (*M. galathea*) and ~ 35 km (*T. sylvestris*) north of the natural range boundaries of these species in areas of predicted climatic suitability.

The dispersal data and population spread rates of both species suggested that the species have only a limited capacity for the long-distance establishment of new populations, even though both species are regarded as more mobile than many other British butterflies species (Asher *et al.* 2001). Natural expansion rates may be faster than we recorded (because more source populations are avail-

able to provide emigrants) but these results are nonetheless consistent with the idea that our study species are moving northwards more slowly than the climate potentially could allow. Despite recorded range shifts for these (Asher *et al.* 2001; Warren *et al.* 2001; Fox *et al.* 2006) and other invertebrate species across the United Kingdom (Hickling *et al.* 2005, 2006), rates of colonization are likely to be lagging behind the climatic changes. Disequilibria between climate and species' distributions may be the norm for the coming century.

Our findings suggest that assisted colonization has the potential to be a useful conservation tool to help limit the impacts of climatic change on species of conservation concern with poor mobility, or whose preferred habitat is discontinuously distributed in a landscape. We also suggest that models relating the distribution of a species to

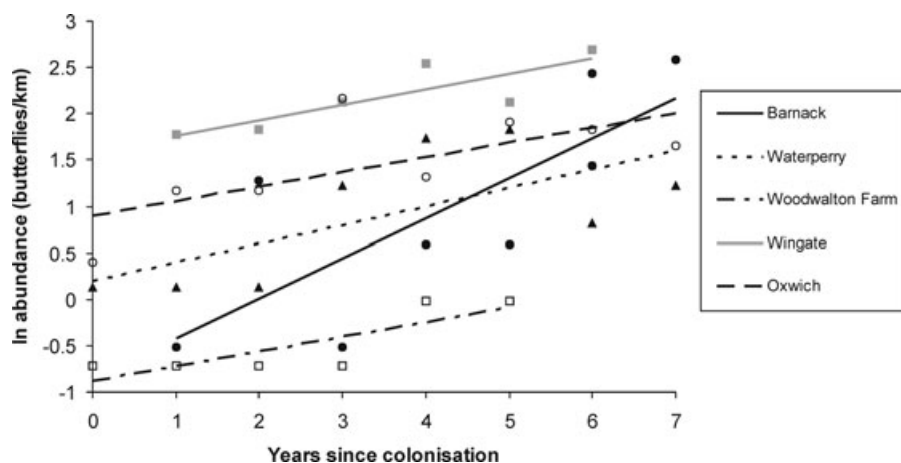


Figure 3 Changes in estimated population index of *M. galathea* at introduced (Wingate—gray squares) and naturally colonized sites (Barnack, U.K. grid ref TF0704—filled circles; Waterperry, SP0069—triangles; Woodwalton Farm, TL2181—open squares; Oxwich, SS4986—open circles). Plotted best fit lines are all significant ($P < 0.05$) and there is no significant difference in slopes.

climate ("climate-envelope" models) are useful in highlighting sites that are potentially climatically suitable for introductions. However, it is important to understand the ecology of a candidate species and recipient communities to avoid introductions into unsuitable areas and to minimize any potential pest problems (Hoegh-Guldberg *et al.* 2008).

In this case, the butterflies were released into communities that contain species with which they already co-exist elsewhere, so negative consequences of the translocations for other species were extremely unlikely. One other major potential issue is whether this approach can ever be cost-effective, which is clearly a major consideration for the assisted colonization of large vertebrates, when an intermediate captive-breeding program is required. In our study, we estimate the total effort (of modeling, release, monitoring, and follow-on analysis) to be in the order of 8 person-months per species, about half of which could reasonably have been carried out by amateurs; other expenses were < £5,000. Although this expenditure might not be justifiable for these widespread species, other than as an experimental study, for threatened species—for which creating habitat and restoring connectivity could be a major challenge—assisted migration may be at least as cost-effective as other adaptation strategies to climatic change.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Recent distribution and regions of predicted climate suitability for *M. galathea* and *T. sylvestris* in the UK

Additional Text: Climate Response Surface Models

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References

- Asher, J., Warren M., Fox R., Harding P., Jeffcoate G., Jeffcote S. (2001) *The millennium atlas of butterflies in Britain and Ireland*. Oxford University Press, Oxford, UK.
- Boitani, L., Falcucci A., Maiorano L., Rondinini C. (2007) Ecological networks as conceptual frameworks or operational tools in conservation. *Cons Biol* **21**, 1414–1422.
- Crozier, L. (2003) Winter warming facilitates range expansion: cold tolerance of the butterfly *Atalopodes campestris*. *Oecologia* **135**, 648–656.
- Fox, R., Asher J., Brereton T., Roy D., Warren M. (2006) *The state of butterflies in Britain and Ireland*. Pisces Publication, Newbury, Berkshire, UK.
- Franco, A.M.A., Hill J.K., Kitchke C., *et al.* (2006) Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries. *Global Change Biol* **12**, 1545–1553.
- Green, R.E., Collingham Y.C., Willis S.G., Gregory R.D., Smith K.W., Huntley B. (2008) Performance of climate envelope models in retrodicting recent changes in bird populations size from observed climatic change. *Biol Lett* **4**, 599–602.
- Gregory, R.D., Willis S.G., Jiguet F., *et al.* (in press) An indicator of the impact of climatic change on European bird populations. *PLoS-ONE*.
- Hickling, R., Roy D.B., Hill J.K., Thomas C.D. (2005) A northward shift of range margins in British Odonata. *Global Change Biol* **11**, 502–506.
- Hickling, R., Roy D.B., Hill J.K., Fox R., Thomas C.D. (2006) The distribution of a wide range of taxonomic groups are expanding polewards. *Global Change Biol* **12**, 450–455.
- Hill, J.K., Thomas C.D., Lewis O.T. (1996) Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: Implications for metapopulation structure. *J Anim Ecol* **65**, 725–735.
- Hill, J.K., Thomas C.D., Huntley B. (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proc Roy Soc Lond B Biol Sci*, **266**, 1197–1206.
- Hill, J.K., Collingham Y.C., Thomas C.D., *et al.* (2001) Impacts of landscape structure on butterfly range expansion. *Ecol Lett* **4**, 313–321.
- Hoegh-Guldberg, O., Hughes L., McIntyre S., *et al.* (2008) Assisted colonization and rapid climate change. *Science* **321**, 325–326.
- Hulme, P.E. (2005) Adapting to climate change: is there scope for ecological management in the face of a global threat? *J Appl Ecol* **42**, 784–794.
- Hunter, M.L. (2007) Climate change and moving species: furthering the debate on assisted colonisation. *Cons Biol* **21**, 1356–1358.

- Huntley, B., Collingham Y.C., Willis S.G., Green R.E. (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE*, **3**, e1439. doi:10.1371/journal.pone.0001439.
- Konvicka, M., Maradova M., Benes J., Fric Z., Kepka P. (2003) Uphill shifts in the distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. *Global Ecol Biogeogr* **12**, 403–410.
- Lensink, R. (1999) Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. *J Anim Ecol* **66**, 811–826.
- McLachlan, J.S., Hellmann J.J., Schwartz M.W. (2007) A framework for debate of assisted migration in an era of climate change. *Cons Biol* **21**, 297–302.
- Menéndez, R., Megias A.G., Hill J.K., *et al.* (2006) Species richness changes lag behind climate change. *Proc Roy Soc Lond B Biol Sci* **273**, 1465–1470.
- Merrill, R.M., Gutierrez D., Lewis O.T., Gutierrez J., Diez S.B., Wilson R.J. (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *J Anim Ecol* **77**, 145–155.
- Midgley, G.F., Hughes G.O., Thuiller W., Rebelo A.G. (2006) Migration rate limitations on climate change-induced range shifts in Cape Proteaceae. *Divers Distrib* **12**, 555–562.
- Parmesan, C., Ryrholm N., Stefanescu C., *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583.
- Parmesan, C., Yohe G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **399**, 579–583.
- Pollard, E., Yates T.J. (1993) *Monitoring butterflies for ecology and conservation*. Chapman and Hall, London.
- Rodgers, A.R., Carr A.P. (1998) *HRE: The home range extension for ArcView*. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
- Root, T.L., Price J.T., Hall K.R., Schneider S.H., Rosenzweig C., Pounds J.A. (2003) Fingerprints of a global warming on wild animals and plants. *Nature* **21**, 57–60.
- Roy, D.B., Rothery P., Moss D., Pollard E., Thomas J.A. (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. *J Anim Ecol* **70**, 201–217.
- Sutherland, W.J., Armstrong-Brown S., Armsworth P.R., *et al.* (2006) The identification of 100 ecological questions of high policy relevance in the UK. *J Appl Ecol* **43**, 617–627.
- Thomas, C.D., Franco A.M.A., Hill J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends Ecol Evol* **21**, 415–416.
- Warren, M.S., Hill J.K., Thomas J.A., *et al.* (2001) Rapid response of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69.
- Wilson, R.J., Gutierrez D., Gutierrez J., Martinez D., Agudo R., Monserrat V.J. (2005) Change to the elevational limits and extent of species ranges associated with climate change. *Ecol Lett*, **8**, 1346–1346.

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